NOTES ON SOME PROBLEMS OF ADAPTATION.

I. On the Re-formation of the Mantle-glands of Chromodoris.[1]

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I.

Upon the ventral surface of the mantle-fold which encircles the body of nudibranchs of the genus *Chromodoris* there is often found, at the posterior end of the fold, a set of small gland-like nodules producing conical elevations of the skin (Fig. 1). With some species these organs may be absent; in others they are relatively invisible during life, becoming more conspicuous, however, at the death of the animal. In *Chromodoris zebra* the glands during life are usually quite obvious, appearing as a number of white conical bodies rather evenly spaced about the margin of the caudal veil. Here, also, they become more prominent at death, due to increased fluid pressure in the tissue surrounding each gland. A similar degree of enhanced prominence, an enlargement of each conical eminence, is induced by intense stimulation of the nudibranch's skin. The glands apparently act as reservoirs of a repugnatorial integumentary secretion. When the animal is strongly stimulated, the secretion may be seen to flow from the terminal pores of one or more of the conical elevations (Crozier, '16). I refer to these bodies as "glands," loosely; the extent of their truly glandular activity is not yet decided.

The number of glands present on the caudal veil of an individual varies considerably, namely from 0 to 19. In connection with an analysis of the ethology of *C. zebra,* I found it necessary to investigate the physiology of these glands, and to study their numerical variations. From this study certain inferences may be derived as to the nature of the processes leading to the

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development of the glands. If these inferences be correct, an interesting parallel is afforded with a law of regenerative phenomena in plants (cf. Loeb, '15; '18*a*; '18*b*).

II.

The outline of the caudal veil is characteristically smooth and approximately semicircular. In a certain number of cases, however, there are apparent in this outline obvious irregularities of a secondary nature. Among the individuals presenting a regular,

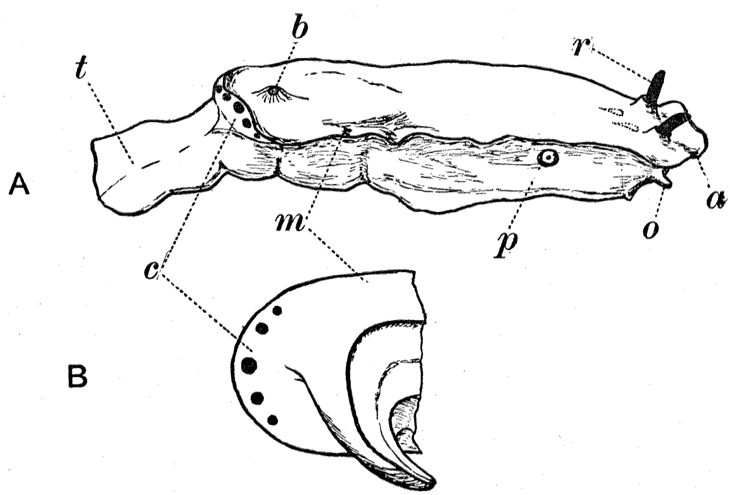

FIG. 1. *A. Chromodoris zebra*, caudal veil (*c*) turned up so as to show the glands (black dots) on its ventral surface; *a*, buccal veil; *b*, branchial collar, contracted over the concealed branchiæ; *m*, mantle folds; *o*, oral tentacle; *p*, reproductive papilla; *r*, "rhinophore"; *t*, "tail" of the foot (× ¾).

B. The caudal veil in ventral aspect, "tail" part of foot turned to one side; this shows a plan of distribution that, on the whole, is the most common.

unindented margin, the number of glands varies from 1 to 16 (Fig. 2). The most common arrangement of the glands is, that one is median, with two on either side of it, all evenly spaced (Fig. 1, *B*). Typically, the five glands in such a set are of about the same size, although in many cases the median gland is the largest.

Although five is the modal number of glands (Fig. 2), other numbers are common; some of these arrangements are illustrated in Fig. 3. Not infrequently one or another gland in an other-

wise symmetrical distribution seems omitted, or suppressed (Fig. 4). It seems possible, if not probable, that each gland may undergo a more or less cyclic sequence of growth and shrinkage.

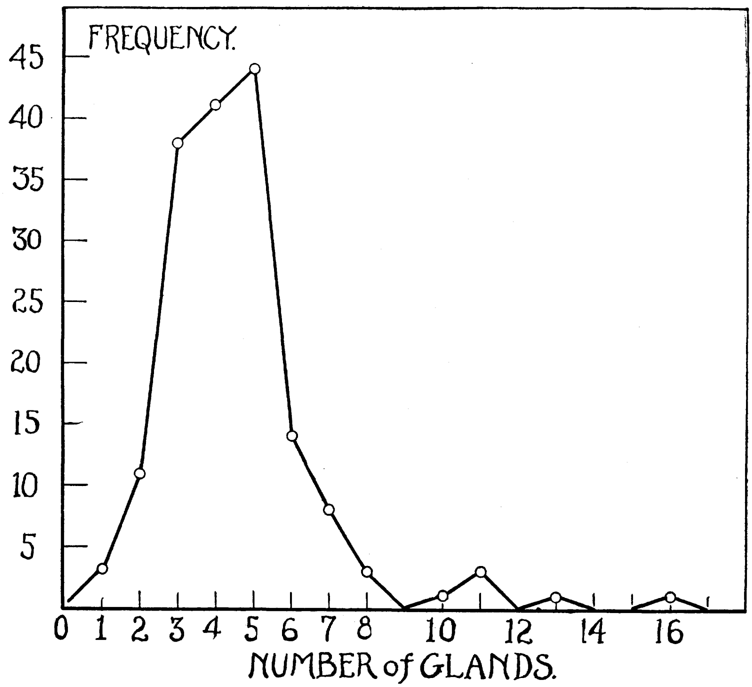

FIG. 2. Showing the frequency with which different numbers of glands occurred in a series of 166 individuals; no obviously irregular sets of glands were included (see text).

Independently of such variations, there is a still further diversity of numbers and sizes among the different sets. As to the number of glands, some examples are given in Fig. 3. In the instances illustrated, and indeed throughout series of several hun-

FIG. 3. Examples of symmetrical sets of "glands" (× 2/3).

dred animals each, examined at different times since 1915, it is generally true that if the number of glands in a set is low, their size is individually larger than in the case of groups composed of greater numbers. Within certain limits, which do not concern

the series of individuals here involved, this is true without reference to the sizes of the nudibranchs. As shown by Fig. 5, the number of glands present in symmetrical sets is independent of the size of the animal.

This leads to the idea that, in general, only a definitely limited

FIG. 4. Examples in which one or more "glands" are omitted (× 2/3).

amount of material is available in each animal for the formation of the white mantle-bodies, regardless of the *number* of these bodies which may be present.

LENGTH, CMS.

NUMBER OF GLANDS.	3	4	5	6	7	8	9	10	11	12	13	14	15	16
0							1							
1						1	1							
2					1	1	3	2	4	1				
3			2	2	8	6	6	7	7					
4	1		1	1	4	8	11	6	7	2	3			
5		2	1	5	13	13	11	6	5	2	3		2	2
6	1				1	7	5	5	2		2			
7				2	1	2	3	2						
8							1		2					
9														
10				1		1								
11								1						
12														
13							1							
14														
15														
16							1							

FIG. 5. Showing the absence of sensible correlation between the *number* of glands on the caudal veil of *Chromodoris* and the *size* of the nudibranch (203 individuals), among instances exhibiting a normal symmetrical distribution of the glands. The column of modal length and the row of modal frequency of glands are enclosed between parallel lines.

III.

A frequency-distribution of the numbers of glands found on different individuals has been given in Fig. 2. In order to avoid certain non-pertinent complications, perhaps resulting in part from seasonal differences (Crozier, '19*a*), I have included in

Fig. 2 only data from one series, obtained September 21–30, 1918. In addition to the individuals involved in Fig. 2, 17 *Chromodoris,* or 9.3 per cent. of the total collected at this time, were

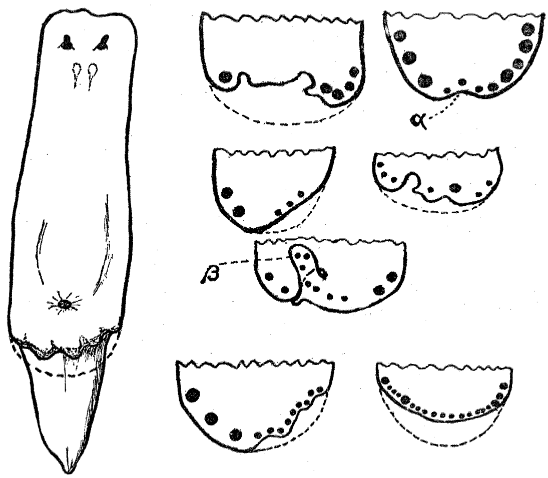

FIG. 6. Showing the character of injuries suffered by the caudal veil, and the results of removal of glands; at α, probably one gland had been removed; at β, a tongue of torn tissue; original outlines approximately as indicated in dashed lines (× 2/3). See text.

seen to have the margin of the caudal veil markedly irregular. Instances of this sort are shown in Fig. 6.

It has nearly always been true in cases of marked irregularity of the caudal mantle that several small glands are situated at

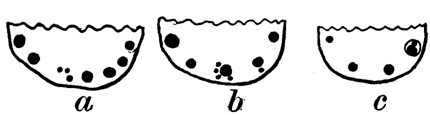

FIG. 7. In *a*, three small glands (surrounding the location of a shrunken gland?); at *b*, a condition which may result from the subsequent enlargement of a gland much shrunken for a time; at *c*, the inclusion (?) of a small gland by an enlarging one normally situated (× 2/3). See text.

points where but one such organ, and that a large one, would characteristically occur. This has been interpreted to mean that if, as the result of injury, one or more glands have been removed, material constantly being transported to these regions is then collected into a greater number of small glands.

It is in fact known that injuries are suffered by the mantle-fold and by other parts of *Chromodoris,* mainly (if not entirely) through the biting of fishes (cf. Crozier, '19*a*). The re-formation of the caudal veil, and with it of mantle-glands, after amputation, has been observed in the laboratory. The process was slow, however (Crozier, '16), occupying some 4 months, and was therefore unsuitable for experimental study; the tissue of the mantle-fold is regenerated very slowly indeed, new glands appearing before an excised region of the caudal veil is restored.

The view here advanced involves the idea that the major portion of the gland-contents, or the precursors of these contents, are in some way carried from distant parts of the animal to the site of the glands. It can be pointed out that the repugnatorial substances contained in the glands are indeed present in the general mantle surface of the nudibranch. Several instances were noted wherein a nudibranch with a much injured caudal veil exhibited 3 or 4 small white accumulations of secretion on the ventral surface of the *buccal* veil. A detailed account of these secretions, with proof of their repugnatorial character and function, I shall provide in another publication.

Microscopically, each gland consists of a spherical sac, tightly packed with oily globules of a special kind, and communicating with the outside by means of a minute pore. In *C. zebra* the histological conditions are not unlike those earlier figured (somewhat incompletely) by Bergh ('98) for *C. juvenca.* Bergh did not observe the pore-like opening, which is difficult to see in sectioned material, and indeed is absent save in mature glands, and at this time the real nature of these structures was unknown. On some other portions of the mantle fold, notably on the ventral surface of the buccal veil, minute white bodies are occasionally seen, which give rise to a similar secretion; these bodies are never so large as the caudal glands.

It has been remarked that each gland may perhaps undergo a process of shrinkage, followed by growth to a maximum size. This might explain such cases as are illustrated in Fig. 7. Materials ordinarily going to a particular gland might, if this gland be in a phase of shrinkage, accumulate in several smaller, new glands about its periphery; subsequent re-growth of the original

gland could then result in a condition such as is shown in Fig. 7, the further development of the new glands being prevented.[1]

IV.

Loeb ('15, '18*a*, '18*b*) has sought to account for certain fundamental characteristics of organ-formation, as seen in *Bryophyllum,* on the basis of a flow of "organ forming" materials. In the case of buds arising from notches in an isolated leaf of this plant, the buds first growing out attract to themselves materials available in the leaf for the growth of buds. The total amount of such materials being limited, the growth of these first buds automatically inhibits the development of others. This explanation has the advantageous support of really quantitative experiments, and it is of interest to notice how closely it may apply to the not very dissimilar phenomena of gland re-formation on the caudal veil of *Chromodoris.*[2]

Regeneration experiments have made it probable that the supply of materials to the region of the glands is so slow that over any given period the total available quantity of such material may be regarded as fixed. The relative sizes of the several glands in a set, in cases where size differences are evident, show that a certain proportion of the gland materials is normally received by each of the (commonly 5) regions of the caudal veil where a gland is characteristically developed. So long as the original glands are present in full activity, no further formation of glands seems to take place. If, however, some of these be removed, the current of secretory materials continues to this region of the mantle and results in the formation of an excessive number of new glands, which individually remain of relatively small size.

[1] A distinct tendency is noticeable for the more anterior glands of symmetrical sets to be smaller than the medial ones, pointing to a bilateral scheme for the distribution of the pro-secretory materials. The exact conditions attending the development of a gland at a particular place can be made clear only from histological study. It seems probable that any portion of the epithelium of the caudal vein *can* give rise to a gland.

[2] Some perhaps analogous phenomena have been described in the growth of previously injured Madreporarians, where normally there is a "dominant apical zooid" (cf. Wood-Jones, '12, p. 112). The manner in which exhausted gland-cells of the amphibian skin are replaced by the enlargement of previously "dormant" cells is also suggestively similar.

The size relations make it clear that what might loosely be regarded as an adaptive over-production of repugnatorial glands subsequent to injury, probably results, on the contrary, from (1) the limited quantity of the repugnatorial precursor substances, and (2) the fact that normally the development of new glands is inhibited through the attraction ("drainage") of these substances by glands already established. This will also explain why in cases where, for example, but 3, rather than 5, "glands" are present on an undamaged mantle, the "glands" are in the former instance individually larger. What it is that determines the number of glands originally formed, remains undiscovered; they are probably absent in all individuals of *C. zebra* less than 1 cm. long.

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